RESPIRATION OF THE SHOOT AS AFFECTED BY TEMPERATURE CHANGES ON THE ROOT

by

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RESPIRATION OF THE SHOOT AS AFFECTED BY TEMPERATURE CHANGES OF THE ROOT[1]

W. H. MICHAELS

(WITH FIVE FIGURES)

MARGINS

Introduction

The effect of temperature upon plant respiration has been extensively studied since the work of DE SAUSSURE and GAREAU, both of whom simply demonstrated that the rate of respiration rose with an increase in temperature. CZAPEK (8), KUIJPER (13), and FERNANDES (10) give extensive reviews of the literature dealing with this phase of respiration. In general it may be said that the rule of Van't Hoff holds for plant respiration between certain limits of temperature, usually considered to be about 5° –25° C. There are a number of exceptions to this rule, however, for example, BENNETT and BARTHOLOMEW (2) found the respiration of potato tubers to be greater at 0° than at 5° C., also that the rule appeared to hold in this case for the rather wide limits of 5°–45° C.

The rate of respiration is by no means constant, even at temperatures which may be optimum for the growth of the organ under investigation. MATTHAEI (18), KUIJPER (13), and FERNANDES (10) have reported marked fluctuations in the respiratory rate, especially at temperatures above 30° C. FERNANDES pointed out that the temperature at which these fluctuations become apparent varies with the age of the seedling, and that the response to temperature varies with different lots of seedlings, even though they be of the same age. BLACKMAN and PARIJA (4), working with individual apples at 22° C., were forced to use two "contour lines" in the graphs presenting their data, in order to indicate the magnitude of the fluctuations in the respiratory rate.

PALLADIN (19), experimenting with etiolated shoots of *Vicia faba*, showed that sudden temperature changes as such acted as stimuli

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upon the respiration rate. WOLKOFF and MAYER (24) had earlier noted that a sudden fall in temperature caused a distinct decrease in the respiratory rate below that normally found at the lower temperature, but a sudden rise had no effect. Gradual fluctuations about a mean had no apparent influence. DETMER (9), ZIEGENBEIN (25), KUIJPER (13), and BLANC (5) all failed to find a stimulation in the respiratory rate as the result of sudden temperature change. They believe the rate of respiration to change gradually with the temperature.

That the temperature of the roots affects the growth of the shoot has been conclusively shown by BIALOBLOCKI (3), BURKHOLDER (6), CANNON (7), and many others, particularly the observations of LINFORD (16), TISDALE (23), and other plant pathologists using the Wisconsin soil-temperature tanks in their studies of the influence of the environment upon the plant and its susceptibility to disease. In general, plants growing in a soil at moderately low temperatures have a larger root system and a coarser heavier shoot than do plants grown at the same air temperature but with a higher soil temperature. The effect of a temperature shock upon the roots in relation to the behavior and future development of the plant does not appear to have been investigated.

LEHENBAUER (14) has briefly but adequately reviewed the work on the effect of sudden temperature changes upon plant growth. It seems established that a sudden temperature change deranges the metabolism of the plant, resulting in either a depression or an acceleration of the growth rate, depending upon the direction and magnitude of the temperature change and also to some extent upon the period of exposure.

Material and methods

Seeds of *Phaseolus vulgaris* (Burpee's Stringless Greenpod) were carefully selected for soundness, and measured to secure uniformity of size. These beans were then germinated in clean quartz sand at 45 per cent of the water-holding capacity. At the end of the third day at 22° C., and before the secondary roots appeared, the seedlings were taken from the sand and their seed coats removed. The roots were carefully thrust through the holes in some no. 5 one-holed rub-

ber stoppers, which were supported over tap water by means of wooden frames. The container in which the seedlings were growing was covered with a larger one that provided ample ventilation and yet shut out the light. All of the seedlings were grown in tap water, which was frequently changed. When the plants were 6–7 days old and their hypocotyls had elongated sufficiently to extend through the stoppers, cotton was packed around them to hold them in posi-

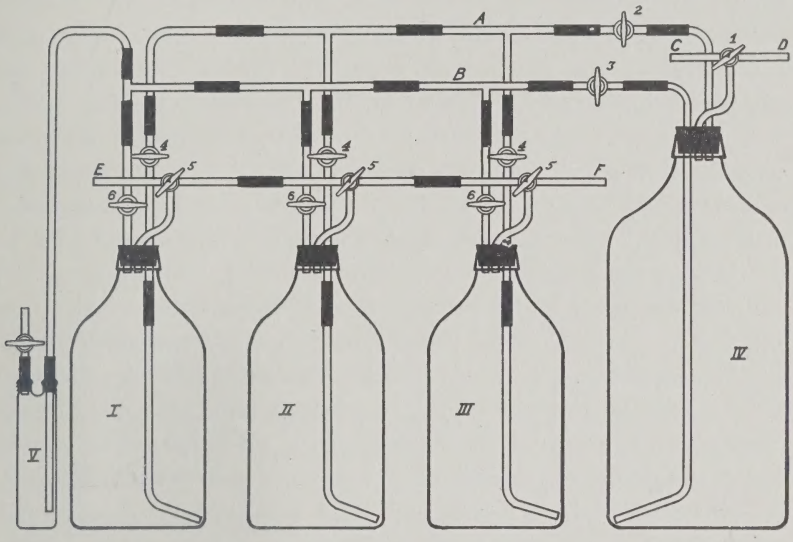


FIG. 1.—Gas collection apparatus

tion. The seedlings were left in this manner until they were needed for experimentation.

The aspirator and gas collection apparatus consisted of two sets of four bottles each, arranged as shown in fig. 1. A vacuum tank, exhausted by an automatically regulated electrically driven pump, maintained the uniform vacuum necessary for suction.

The gas collection apparatus was filled with a liquid which absorbed little or no carbon dioxide. The solution used was that of Layng and Crum, as reported by HOTTES and HAFENRICHTER (12). This liquid consists of a 35 per cent aqueous solution of zinc sulphate to which 14 gm. of concentrated sulphuric acid per liter of solution is added. Considerably more pressure or suction is needed to force

or draw this liquid through the apparatus than is required for water, but in spite of this difficulty it has proved very satisfactory.

Each of the bottles I, II, and III has a capacity of 4 liters, while the capacity of bottle IV is 12 liters. Stopcocks 2, 3, 4, and 6 all have a 2 mm. bore. It was found necessary to use stopcocks of this size when it was desired to aspirate at the rate of 3 or 4 liters in 10 minutes; at slower rates of aspiration stopcocks of 1 mm. bore should prove satisfactory. The three-way stopcocks, which serve for the passage of gas only, are of 1 mm. bore. Heavy pure gum rubber tubing was used on all joints, the rubber connections and stoppers being wired into place. Bottle V served as a safety valve.

To aspirate, stopcock 1 is turned to connect bottle IV with the vacuum through *D*, and stopcock 2 opened. Next stopcock 4 is opened on the bottle in which it is desired to collect the gas, in this case bottle I. The three-way cock 5 is then turned to connect the bottle with the respiratory chamber through *E*. The vacuum of 6 cm. now draws the liquid out of bottle I through tube *A* into bottle IV, and as the level of the liquid falls in bottle I the gas from the respiratory chamber is drawn into it. The speed of aspiration may be governed by the insertion of a piece of capillary tubing of the proper bore into tube *A*, between stopcock 2 and bottle IV. At the end of the period of gas collection stopcock 4 is closed and 5 turned to seal bottle I but to permit a through passage from *E* to *F*. For continuous gas collection, stopcocks 4 and 5 on bottle II should be opened before cocks 4 and 5 on bottle I are closed. With tight connections no solution can be withdrawn from bottle II until cock 5 on bottle I is turned to permit a through passage from *E*. If it is desired to have a period of aspiration between gas collections, it can easily be accomplished by attaching the vacuum, properly reduced, to *F*. In any case it is best to have the vacuum attached here at all times, to minimize the chances of inadvertently admitting air to the system by turning the wrong stopcock. The same procedure is then followed with bottles II and III.

To measure the volume of gas collected and to take a sample, the tube connecting the respiratory chamber with *E* is removed and replaced by one leading to the gas meter. The tube connecting with the vacuum at *F* must either be removed or the vacuum shut off.

Stopcock 2 is now closed and cock 1 turned to connect with the air pressure line through *C*. The air pressure was maintained at 150 gm. per square centimeter. Stopcock 3 is opened, followed by stopcock 6 on bottle I, and lastly cock 5 is turned to connect bottle I with the gas meter through *E*. As the liquid is now forced out of bottle IV into bottle I, the gas is forced out of bottle I through the meter. The sample was taken as the gas left the meter.

The gas meter used was one designed especially for respiration work, and was graduated to hundredths of a liter but permitted accurate estimates to thousandths. The samples were taken with the type of sampler described by BAILEY (1), and the gas analysis was made with BAILEY'S modification of the Haldane-Henderson gas apparatus. All gas volumes were reduced to the dry state at 0 °C. and 760 mm. mercury pressure. The weight of carbon dioxide in milligrams was obtained with the aid of the table of densities given by PARR and KING (20). Five place logarithms were used throughout.

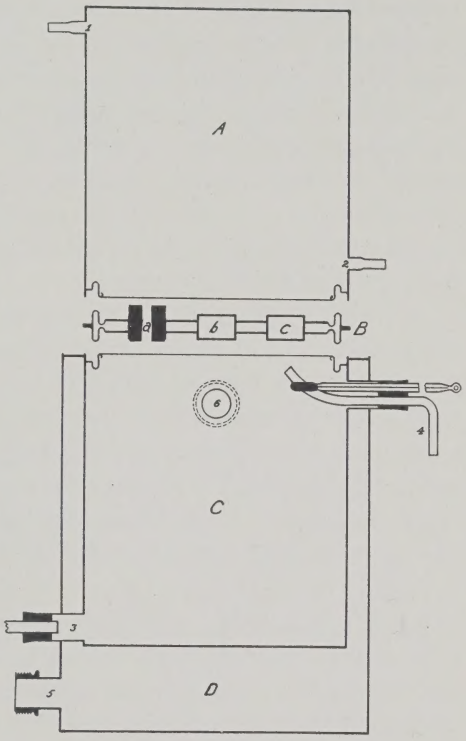


FIG. 2.—Respiration chamber: *A*, respiration chamber proper (1, 2, inlet and outlet respectively); *B*, double lid (*a*, *b*, *c*, brass tubes through lid and a rubber stopper inserted in *a*); *C*, inner root chamber (3, inlet and outlet tube; 4, overflow tube with thermometer inserted above); *D*, outer root chamber (5, 6, hose connections through which cooling liquid was circulated between *C* and *D*).

The respiration chamber is shown diagrammatically in fig. 2. It consisted of two parts, the respiration chamber proper (*A*), and the chamber in which the roots were held (*C*). Both were good quality

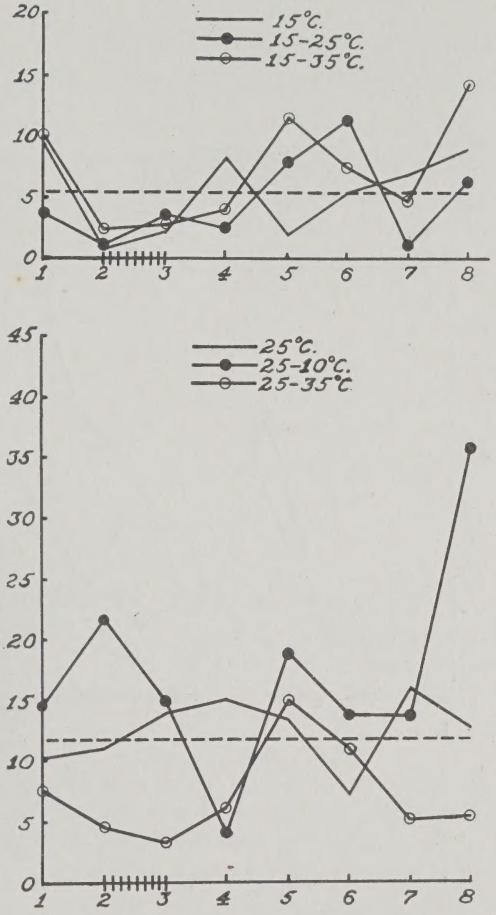
4-liter tin cylinders with tightly fitting pry lids. The lids were soldered together (*B*), seven holes punched through them, and short brass tubes soldered into these openings (*a*, *b*, etc.). The plants in their no. 5 stoppers were later forced into these tubes. The respiration chamber was thus inverted over the root chamber, which was soldered into a larger tin cylinder (*D*), making a double-walled chamber. Water or brine was circulated in the space between the two cylinders to control the temperature of the roots. An opening (3) was also provided in the root chamber, by means of which the water in which the roots were growing could be rapidly changed. The second opening in the root chamber carried an overflow tube (4) and a thermometer. The respiration chamber proper had two openings, an inlet tube (1) near the upper end of the cylinder and an outlet tube (2) near its lower extremity.

By means of this apparatus it was possible to increase or decrease the temperature of the water in which the roots were growing in about 6 minutes. During the entire test the respiration chamber was kept in one of the constant temperature cases which are standard equipment in the laboratory. The range of temperature fluctuation within the case was 1°. The air entering the respiration chamber was drawn through a Truog absorption tower filled with shell-caustic and then through a Winkler tube filled with 40 per cent potassium hydroxide.

When ready for an experiment, the seven selected seedlings in their rubber stoppers were forced into the holes in the double lid and the cotton removed from around the plants. Next the plants were sealed into the stoppers with chewing gum. Gum was the only seal found which did not injure the plants but would withstand the necessary vacuum. After the gum had set, the rim of the lid was lightly greased with stopcock lubricant and the respiration chamber proper forced into place. The lid was then loosened from the lower can and the chamber tested under 2.5 cm. vacuum for about 5 minutes. The respiration chamber was then placed in the temperature case and the connections with the aspirator and absorption tubes made.

The plants were always placed in the case at five o'clock of the afternoon before the test and a slow rate of aspiration maintained

all night. The actual test was begun either at seven or eight o'clock the following morning. At the end of the experiment the plants were removed from the chamber, any adhering gum washed off with alcohol, and the plants placed in the drier in preparation for the dry weight determination. All of the experiments were run in duplicate or triplicate, and the data are recorded on the basis of the dry weight of the seedlings at the end of the experiment. A total of 25 experiments, using seven seedlings each, were run. The values recorded in table I represent the averages of 194 carbon dioxide determinations and approximately 500 gas analyses.



FIGS. 3, 4.—Fig. 3 (above), respiration rates of seedlings of 15° C. group; fig. 4 (below), respiration rates of 25° C. group of seedlings; all values from table I (abscissae represent time in hours; cross-hatched portion indicates time roots were at second temperature; ordinates represent mg. CO_2 emitted per hour per gm. dry weight).

Experimentation

The data for each temperature series are presented in table I and figs. 3, 4, and 5. The dotted horizontal line through each graph represents the total average rate of respiration per hour per gram dry weight at the constant temperature of the group. These average rates of respiration are 5.34 mg. of carbon dioxide per hour at 15° C.,

11.43 mg. of carbon dioxide at 25° C., and 8.35 mg. of carbon dioxide per hour at 35° C. In those experiments in which the temperature of the water in which the roots were growing was changed, the change was made at the beginning of the third hour and the return to former temperature was at the beginning of the next hour. The cross-hatching of the abscissae indicates the period during which the roots of the plants were at the changed temperature. In the designation of any series in which two temperatures are used, the second temperature indicated always refers to the one to which the roots were changed during the third hour.

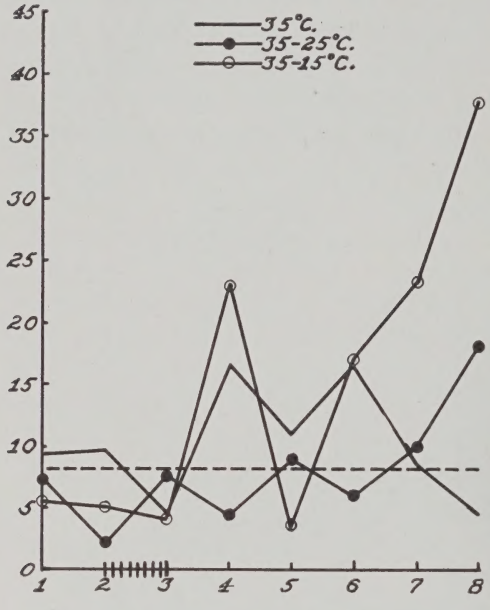


FIG. 5.—Respiration rates of seedlings of 35° C. group, all values from table I (abscissae represent time in hours; cross-hatched portion indicates time roots were at second temperature; ordinates represent mg. CO_2 emitted per hour per gm. dry weight).

15° C. GROUP.—The data for the 15° C. group are shown graphically in fig. 3. A striking feature is that all of the curves show a falling respiratory rate for the first 2 hours. The most logical explanation would appear to be that there had been a slight accumulation of carbon dioxide in the respiration chamber during the night, due to a slower aspiration rate; however, since the same rate was used throughout all of the experiments, one would expect the same type of declining curve at 25° and 35° C., but it is present in only one or two cases at these temperatures. The writer is unable to explain the coinciding of these curves. The 15° C. constant temperature curve is notable mainly for its rather wide fluctuations from the mean. The chief difference noticeable between the 15°–25° and 15°–

35° C. curves is that the former rises during the time that the roots are at the warmer temperature, while the latter remains at a uniform level. The shock of the change to 35° C. seems to have been severe enough to cause the respiratory process to remain on a level with that of the previous hour. The 15°–25° C. curve, on the other hand, rises during the third hour, probably because the temperature change is too small to depress the respiration rate for the entire hour. This curve shows a decrease in the respiration rate for the fourth hour, apparently due to the effect of the sudden change back to 15° C. The 15°–35° C. curve shows no signs of a second shock.

TABLE I

RESPIRATION RATES OF ETIOLATED BEAN SEEDLINGS, 7–9 DAYS OLD, WHEN SUBJECTED TO DIFFERENT TEMPERATURE TREATMENTS, IN MG. CARBON DIOXIDE PER HOUR PER GM. DRY WEIGHT

HOURS OF EXPERIMENTATION	15° C. GROUP			25° C. GROUP			35° C. GROUP		
	15°	15°–25°	15°–35°	25°	25°–10°	25°–35°	35°	35°–25°	35°–15°
1.....	9.48	3.58	10.26	10.19	14.29	7.59	9.28	7.84	5.37
2.....	0.77	1.05	2.47	10.93	21.67	4.64	9.68	2.25	5.04
3.....	2.02	**3.52***	**2.69***	13.92	**14.90***	**3.26***	4.58	**7.89***	**4.02***
4.....	8.13	2.56	4.17	15.09	4.03	6.07	16.44	4.23	23.15
5.....	1.97	7.97	11.56	13.08	18.90	14.94	11.03	8.73	3.31
6.....	5.44	11.65	7.52	7.16	13.66	10.93	16.51	6.07	16.74
7.....	7.05	0.89	4.77	15.82	13.66	5.04	8.48	10.02	23.35
8.....	9.02	6.33	14.49	12.67	35.74	5.42	4.31	18.06	37.56

* Hour at the changed temperature.

The difference between these two curves is more easily understood when it is remembered that 25° C. is optimum temperature for the bean plant.

25° C. GROUP.—Fig. 4 presents the averages for the 25° C. group. All of the curves for the experiments in which the temperature was changed show a fall during the third hour, which in the 25°–10° C. series is continued in the fourth hour. That the temperature change acted as a stimulus is indicated by the remarkable rise in the eighth hour of the 25°–10° C. series. Changing the roots from 25° to 35° C. flattened the curve between the second and third hour. The curve then rises, the maximum rise being during the fifth hour.

35° C. GROUP.—The greatest fluctuations in the respiration rate of the entire study are found in this group. Fig. 5 presents the curves

for the various series. The large stimulation shown by the 35°–15° C. curve is probably due to the 20° difference between the two temperatures used. Again the temperature change has flattened the curve for the hour at the changed temperature, and is followed immediately by a rapid rise. The 35°–25° C. curve indicates that this temperature change had little effect other than to depress the respiration rate for the four or five hours following the change. It is impossible to say that there was any shock effect in this case.

Discussion

These experiments indicate that sudden temperature changes upon the roots of etiolated bean seedlings produce a shock which is transmitted to the shoot, as evidenced by its changed respiratory rate. The magnitude of the shock does not appear to be in proportion to the difference between the two temperatures employed. This is brought out by a comparison of the curves for the 15°–35°, 25°–10°, and 35°–15° C. series. The 15°–35° and 35°–15° C. series received shocks of identical magnitude, yet the former shows comparatively little shock effect while the latter shows the greatest effect of the entire group of experiments. Further, the shock shown by the 25°–10° series is greater than that for the 15°–35° C. series. These facts seem to indicate that the direction of the shock is more important than its magnitude.

In a general way this conclusion is borne out by PALLADIN'S (**19**) results. He found an increase of 53 per cent in the amount of carbon dioxide given off over that of the control series, when the etiolated *Vicia faba* shoots floating on saccharose solution, which had been at a temperature of 36°–37.5° for several days, were tested at 18°–22° C. Similar shoots floating on saccharose solution transferred from 7°–12° to 18°–22° C. showed an increase of only 40 per cent in their carbon dioxide output. In this case the range of temperatures was also different, however, there being about 18° difference between the medium and high temperatures, and only about 9° C. difference between the medium and low temperatures. The response was certainly not in proportion to the temperature difference, but it is impossible to say definitely that the direction of the change influenced it.

A study of the graphs of the various series shows that the 25° curve has fewer sharp fluctuations than either the 15° or the 35° C. curves. The 25° plants were at a temperature which is very near their optimum temperature for growth. Apparently their metabolic processes were going on at a uniform rate, the equilibrium of which is hard to disturb. This was not true for the other two groups. These results are contrary to the work of most investigators, who have found that the rate of respiration is more uniform at lower temperatures than it is at medium or high temperatures.

The type of response to the temperature change also varies. Thus in the 15° group and the 25°–35° C. series the curves showing the respiration rate are comparatively flat from the second to the fourth hours. For the 25°–10° and the 35°–15° C. series the curves begin to fluctuate after the third hour instead of the fourth. These last two series also show the greatest range of fluctuations of the entire group of experiments, consequently the difference in type of response must also vary with the effectiveness of the stimulation.

The marked depression in the average respiratory rate at 35° C. seems largely due to the action of a "time factor." It must be remembered that the average respiratory rates, indicated by the dotted lines in figs. 3, 4, and 5, represent the rate of respiration after approximately 14 hours' exposure to the respective temperatures. The magnitude of the depression may be seen when the values of Q_{10} for the present data are compared with the results obtained by KUIJPER (13) for pea seedlings, and by LUNDEGARDH (17) for the leaves of the potato plant. KUIJPER'S respiration results are based on the first hour at these temperatures, while those of LUNDEGARDH cover a period 5–17 minutes. These results are:

Temperature	15° C.	25° C.	35° C.
Q_{10} of present data	2.14	0.70	
Q_{10} of KUIJPER'S data	2.34	1.58	
Q_{10} of LUNDEGARDH'S data	2.20	1.30	

Plainly the value of Q_{10} for the 10° between 25° and 35° C. in the present experiments is much lower than in the other two cited.

The present experiments also indicate clearly the close connection between the activities of the shoot and those of the root. By just what means a shock administered to the cells of the root is trans-

mitted to the cells of the shoot is impossible to say at present. SNOW (21) and others have advanced the idea that a hormone or similar substance is formed as the result of a stimulus, and is then carried to all parts of the plant. Others believe that the stimulus is of an electrical nature, and passes from cell to cell by means of the slender connecting strands of protoplasm or plasmodesma.

Regardless of the method of conduction, it is certain that in this case a stimulus acting upon the root has affected the metabolism of the shoot. From this it might be concluded that a stimulus acting upon one part of the plant will influence the entire plant. That this is not always the case is illustrated by the various treatments used to break up the rest period of woody plants, in which only the portion of the plant actually treated has its rest period broken. Similarly, GARNER and ALLARD (11) have found localized response to length of day in cosmos. It is realized that these cases are not exactly comparable with the present experiments, for here we are dealing with the effect of a stimulus upon a portion of a plant which could be separated from the remainder of the organism without seriously injuring it. It seems, therefore, that the effect of a stimulus acting upon the entire root or shoot is different in respect to transmission from the effect if it had acted upon only a small portion of the plant.

The action of the stimulus may perhaps best be understood by a consideration of the cell and its metabolism. A number of investigators consider the cell as a colloidal complex in which the various chemical reactions proceed. SPOEHR (22) has expressed this concept as follows:

> It seems highly improbable that the life processes consist of any one series of chemical changes or are dependent upon any particular molecule or chemical group. But rather the simple life processes entailing energy changes may perhaps be regarded as a complex of interrelated chemical changes taking place in a certain medium or substratum. This medium, colloidal dispersion, mixture, or aggregate of various substances is the seat or substratum in which the various chemical reactions take place, the nature and course of which are determined by the complex of properties associated with water control, surface phenomena, and of course catalysts (such as inorganic salts and enzymes). These colloids do not enter into or support the chemical reactions or do so probably only in a rather indirect manner, serving primarily as a physical medium. Such a system would be of a heterogeneous nature and, of course, of the most complex type,

and capable of various adsorption phenomena productive of localized action which would influence the function as well as the structure of the system. In fact, such a hypothesis would demand that the substratum be relatively stable, that the colloidal material once formed does not break down as readily as the other substances, or only after the supply of these has been exhausted. This does not mean actual or chemical stability, but rather relative to the other substances under the existing physiological conditions, as, for instance, relatively slightly dissociated by salts or other catalysts and resistant to the action of enzymes.

Plant respiration is at present conceived to be a complicated life process which takes the form of a chain of catalytic reactions in which the products formed by one reaction become the reactants in the next link. These reactions, in general, follow the law of mass action which in its simplest form states that the rate at which any reaction proceeds is directly proportional to the amount, or rather the concentration, of the reacting substance. In other words, any change in the amount of one of the reactants brings about the establishment of an entirely new equilibrium, with a resulting increase or decrease in the amount of end product. Further, there is the probability that the individual steps may respond differently to external influences, for example, they might have different temperature coefficients, in which case a rise in temperature might accelerate one link more than the others, resulting in an excess of its end product; or a lowering of the temperature might retard one reaction more than the others. This reaction would then become the limiting factor in the series.

Does the stimulus of these experiments act directly upon this chain of reactions by changing the speed of one or more links, or does it act indirectly by first influencing the structure of the protoplasm? These two viewpoints are not necessarily opposed. Enzymes are very sensitive to temperature, and it is entirely probable that the temperature change has affected the rate of enzyme activity directly, thus changing the speed of one or more links in the chain of reactions. On the other hand, a number of modern workers incline to the view that protoplasm has a definite structure, and that the reactions proceed at the interphase boundaries. Lillie (15) states:

Since the formation of films is a characteristic feature of the processes at phase boundaries in polyphasic systems of all kinds, and especially in protoplasm, it is probable that films are present at all sharply defined boundary

surfaces in the living cell, i.e., not only at the general surfaces of the cell and of cell structures like nuclei and vacuoles, but also at the surfaces of fibrils, granules, chromosomes, mitochondria, the Golgi apparatus, and other structures. Variations in the physical or chemical properties of these films will influence the catalytic and other properties of the surfaces, and hence the nature and rate of the chemical reactions occurring in the cell under the surface influence. Electrical factors are of special importance in all such effects; . . . . Since these films are readily broken down and reformed under often slight changes of condition, the state of the protoplasmic surface layers is subject to continual change; the rate and character of the chemical reactions occurring under the influence of these surfaces are affected correspondingly. There are many indications (apart from the action of narcotics) that the special sensitivity of the protoplasmic system to chemical, electrical, and other changes of condition, i.e., its irritability, is to be referred chiefly to this variability of the protoplasmic films.

It seems clear that any change in the rate of one of the steps in the chain of linked reactions, as the result of a stimulus, would influence the entire chain and consequently result in a changed amount of carbon dioxide being released. This explanation will satisfactorily explain the change in respiratory rate upon a change in temperature, but it will not explain the constant fluctuations in the respiratory rate just noted. The continual breaking down and building up of protoplasmic films, with the resulting changes in surface action, would seem to offer a more probable explanation for these fluctuations. Probably both of these processes are concerned. Protoplasm undoubtedly has a definite structure, for the mere presence of the chemical and physical components usually found in the cell does not produce a living cell. Further, when the structure of the cell is destroyed, profound physical and chemical changes at once appear. On the other hand, many of the chemical reactions proceeding within the cell have already been established. Thus both explanations have a sound basis in fact.

Summary

1. A definite stimulation of the respiratory rate of the shoot is shown to occur as a result of temperature change of the root.

2. The amount and type of stimulation vary with the temperature at which the plants are held and the direction of the temperature change.

3. The magnitude of the stimulation does not appear to be defi-

nitely related to the size of the difference between the two temperatures used.

4. The 25° C. constant temperature series shows smaller fluctuations from its mean respiratory rate than does either the 15° or the 35° C. constant temperature series.

5. A study of the temperature coefficients shows that a marked depression in the respiratory rate occurred at 35° C., probably due to a "time factor."

6. A new type of aspirator and gas collection apparatus is described.

The writer wishes to acknowledge his indebtedness to Professor CHARLES F. HOTTES, under whose direction the investigation was undertaken, for his aid in the construction of apparatus and for his most helpful criticism and suggestions during the progress of the work.

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